THE PERIODICITY OF FRESHWATER ALGAE*

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The normal life of a freshwater alga such as a Spirogyra consists of a period of germination of spores, a period of growth and development, and a period of sexual or asexual reproduction, commonly followed by a period of dormancy. An Oedogonium has in addition to these periods one or more phases during the vegetative period when zoospores are produced. Other green algae have part or all of these several periods. Consequently if we follow the changes in the algae occurring in a given pond or stream throughout the year, we find a rather regular succession of life phases for each of the species present. Since the life cycles of the different species vary in their duration, we also find an orderly sequence of appearing and disappearing species.

To discover the causes underlying these periodic changes, efforts have been directed in two rather distinct lines of investigation: (1) The observation of algae under laboratory conditions, and (2) The observation of algae under natural conditions.

To the first class belong the investigations of Klebs, Artari, Benecke and Danforth. These experiments have given us a considerable body of information concerning the effects of light, temperature, concentration and the chemical nature of the medium. The results of the experiments with variations in light and temperature as factors in accelerating or retarding vegetative and reproductive activities are for the most part qualitative. They still await a quantitative statement of their relations. The experiments with concentration and chemical composition of the medium not only show very inharmonious results, but the conclusions to which they have led are scarcely applicable to the explanation of the periodicity of algae in nature, since the concentrations used are many times the concentrations of our natural waters, and many of the substances used do not occur in our pond and stream solutions. These results may be of great interest in cell physiology, but they do not appear to be applicable to the conditions out of doors.

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The second source of information is the study of algae in the field. Comere studied the algae of the vicinity of Toulouse, France. In addition to a classification of the habitat groups of algae, he classified the local species into seasonal groups on the basis of their times of reproduction alone. Fritsch and West in England have contributed a number of papers dealing with the frequency and reproductive activities of the algae in a number of pools and ponds. Some of the records of Fritsch cover a period of five years and are correspondingly valuable. In this country Copeland made a two-year study of the periodicity of the Spirogyras, and Brown published some records of the occurrence of algae in southern Indiana.

As a result of these field studies there have developed two extreme points of view: Copeland came to the conclusion that his observations "offer overwhelming evidence in support of the view that the phenomenon of conjugation results not so much from external as from internal conditions," and "that Spirogyra has definite periods of growth and reproductive activity"; Fritsch on the other hand assumes to account for all the phenomena of germination, vegetative development and reproduction on the basis of changes in the environment. He emphasizes especially the effects of temperature, light, and concentration of medium, although he made no determinations of the actual concentration of the waters with which he dealt.

The present paper is based on seven and a half years continuous records of the algal conditions in central Illinois. About 3,000 collections have been analyzed. Particular attention has been given to the Zygnemales, the Oedogoniales, and the other filamentous forms. As a result there are notes on the occurrence of over three hundred species, and sufficient data to establish the periodicity curve of about half that number. Aplanospores, zoöspores, zygospores and oöspores have been recorded more than a thousand times in the course of the work.

Our algae fall with few exceptions into six natural groups, based on the time of their germination, vegetative development, reproduction and dormancy (Fig. 1).

1. The *Winter Annuals* begin their vegetative activities in the autumn, increase these activities up to the time the ponds are frozen over, and pass the winter under the ice. They may develop further during protracted winter thaws and may even fruit. Their reproductive activities culminate in March and April, although sexual spores

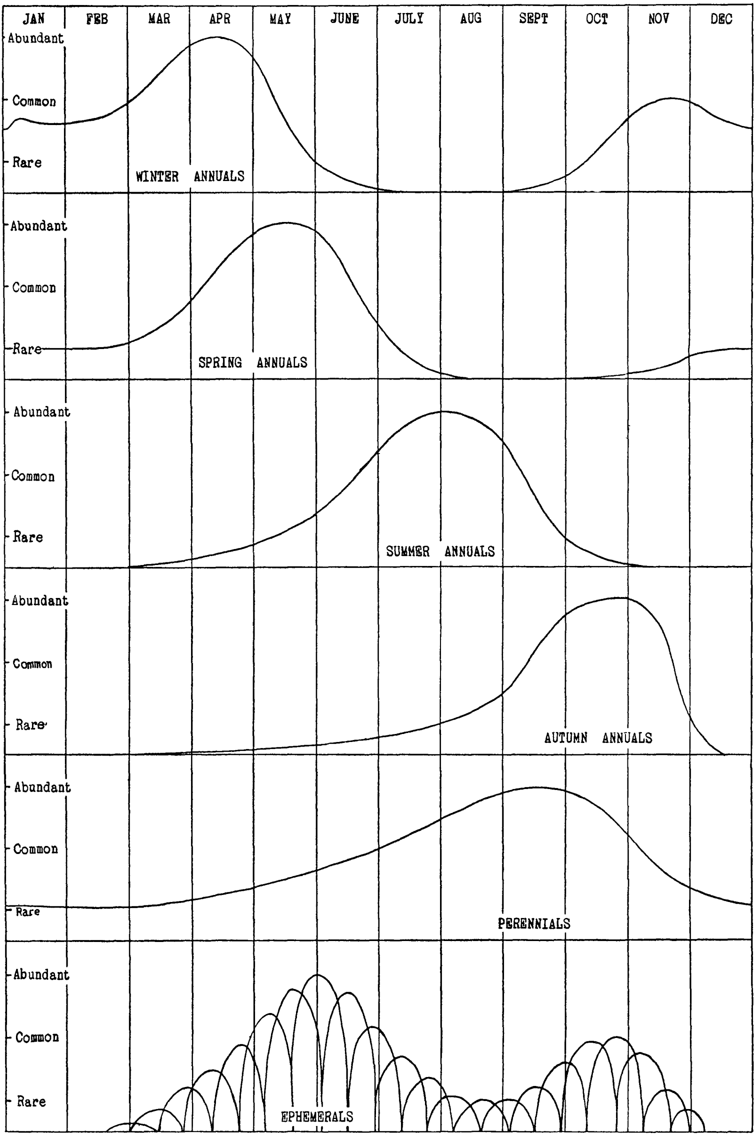

FIG. 1. Curves of frequency of the six ecological groups of algae.

may be produced at any time from November to April. Zoöspores are formed during the period of vegetative development, and aplanospores and akinetes during the period of decline. Prominent among the winter annuals are: *Conferva minor* Klebs, *C. bombycina* Agardh, *C. utriculosa* Kütz., *Vaucheria geminata* (Vauch.) DC., *V. sessilis* (Vauch) DC., *Draparnaldia plumosa* (Vauch.) Ag., *Tetraspora lubrica* (Roth) Ag., *Stigeoclonium lubricum varians* (Hazen) Collins, *Gomphonema angustatum* Grun., *G. acuminatum* Ehrb., *Spirogyra tenuissima* (Hass) Kutz., *S. inflata* (Vauch) Kütz. and *Oedogonium rufescens* Wittr.

2. The *Spring Annuals* begin their vegetative period in late autumn or early spring, attain their maximum development and the reproductive stage during May. This is by far the largest of the seasonal groups. Among the common forms are: *Zygnema stellinum* (Müll.) Ag., *Z. leiospermum* De Bary, *Z. insigne* (Hass.) Kütz., *Spirogyra catenaeformis* (Hass.) Kütz., *S. varians* (Hass.) Kütz., *S. protecta* Wood, *Mougeotia scalaris* Hass., *M. robusta* (DeBary) Wittr., *Oedogonium echinospermum* A. Braun, *Oe. multisporum* Wood, *Oe. suecicum* Wittr., *Bulbochaete crassiuscula* Nordst., *Debarya decussata* Transeau, *Vaucheria hamata* (Vauch.) DC., *Draparnaldia Ravenellii*, Wolle, *Coleochaete scutata* Breb., and *Herpesteiron confervicola* Naeg.

3. The *Summer Annuals* germinate in the spring. The greatest reproductive activities occur in July and August. Zoöspores are most frequent in spring and early summer. Aplanospores develop mostly in August and September. Among the common summer annuals are *Oe. praticolum* Transeau, *Oe. varians* Wittr., *Oe. vaucherii* (LeCl.) Braun, *Calothrix stagnalis* Gomont, *Spirogyra ellipsospora* Transeau, *S. nitida* (Dillw.) Link, *S. irregularis* Nägeli, *S. setiformis* (Roth) Kütz., *Mougeotia sphaerocarpa* Wolle, and *Cylindrocapsa geminella minor* Hansgirg.

4. The *Autumn Annuals*. These species begin their vegetative development in late spring, increase through the summer and have their maximum abundance in the autumn. Sexual reproduction if present, occurs mostly in September and October. This is a comparatively small group, and includes *Rivularia natans* (Hedw.) Welw., *Oedogonium capilliforme* Kütz., *Oe. macrandrium* Wittr., *Oe. obtruncatum* Wittr., and *Oe. crassum amplum* (M. & W.) Hirn.

5. The *Perennials*. This group includes species whose vegetative cycle may be or is continuous from year to year, in permanent streams and ponds. Reproduction may occur at any time in some of the

forms, but in general is more abundant during May and June. Some local examples of perennials are *Rhizoclonium hieroglyphicum* (Ag.) Kütz., *R. fontanum* Kütz., *Cladophora glomerata* (L.) Kütz., *C. fracta* (Dillw.) Kütz., *Pithophora varia* Wille, *Tolypothrix tenuis* Kütz., *Hyalotheca dissiliens* Breb., *Desmidium swartzii* Ag., *Mougeotia genuflexa* (Dillw.) Ag. (in permanent ponds) and *Zygnema pectinatum* (Vauch) Ag. (in permanent ponds).

6. The *Ephemerals* are species having vegetative cycles of a few days or at most a few weeks' duration. Generations succeed one another rapidly during the periods of favorable conditions. These species are mostly plankton and soil algae. Zoöspores are the usual means of reproduction, and aplanospores and akinetes carry them over the unfavorable seasons. Some examples of ephemerals are *Botrydium Walrothii* Kütz., *Ineffigiata neglecta* W. & G. S. West, *Pediastrum Boryanum* (Turp.) Meneg., *Scenedesmus quadricauda* (Turp.) Kütz. and *S. bijuga* (Turp.) Wittr.

The recognition of these classes is of ecological interest because of the greater ease of description of the life habits of a particular species. In the present connection it is of importance because the finding of great irregularity in the behavior of some form or group of forms may suggest the causes correlated with the irregularity, or a method of experimentation which will lead to the causes. I believe that the most prolific source of contradictory results among experimenters has been a lack of knowledge of the normal periodicity of the algae in the field, and the failure to appreciate the importance of the time of germination and the vegetative age of the materials used in the experiments. I have hoped throughout this study of the behavior of algae in the field, that it might furnish new points of departure for experimentation.

The other results of these field observations may be conveniently presented under four heads: (1) The time and conditions of germination, (2) the vegetative cycle, (3) the reproductive period in relation to external conditions, and (4) the method of reproduction in relation to heredity and external conditions.

Germination.—The vast majority of zygospores, oöspores and aplanospores germinate in the spring. But the period during which the spores of a particular species germinate is often extended over several weeks. This is indicated both by field observations and laboratory experiments. Further, there is some germination going on

at all times of the year, a secondary maximum occurring in September and October. In the years with heavy autumn rains this is especially marked. The temperature as a control of the germination of algal spores has probably been overestimated. The spores of many species will germinate at all the ordinary water temperatures. There is still less reason for speaking of the germination as coincident with "rising" or "falling temperatures." The data in hand point rather to the conclusion that all those factors which contribute to the germination of seeds are also operative here. Increased oxygen content of the water, increased mineral content, and induced changes in the permeability of the spore coats are probably the controlling factors, the speed of germination being retarded or accelerated by the temperature.

Length of the Vegetative Cycle.—So far as I am aware this has received scant attention among experimenters. In some forms like Pithophora and Vaucheria it is probably of no consequence for they may be induced to fruit immediately upon germination. But in other forms like the Zygnemales and Oedogoniales it is probably of vital importance in the interpretation of experimental results. In these forms the vegetative cycle is a period of the formation of the filament by cell division, and the period of accumulation of nutrient and other materials. During this period photosynthesis, proteinsynthesis and assimilation are active on the one side, while respiration, accumulation and growth are active on the other. Field observations and experimentation indicate that this must go on for a certain length of time before reproduction is possible. They also indicate that the speed of the metabolic processes must attain a certain minimum rate or reproduction fails to close the vegetative cycle. A number of factors may limit the speed of metabolism; light of low intensity is obviously one that operates so effectively, that algae in shaded portions of streams may never reproduce, or even be able to maintain more than a temporary existence. It is probable that excessively high temperature may also prevent the normal development of the algae. Higher temperatures accelerate and lower temperatures retard the completion of the vegetative cycle. These results are just as clearly indicated by field observations as by experiment. The amounts of available oxygen and carbon dioxide in the water also act as limiting factors to these processes.

The length of the vegetative cycle is so regular from year to year, that, given the conditions, it is not difficult to predict the order in

which the species occurring in a particular pond will fruit. If we take one of the larger genera like Oedogonium, Spirogyra or Zygnema, we find a remarkably regular annual succession of species. In a general way there is an evident correlation between the length of the vegetative phase and size of the cells. In the case of the Spirogyras I have attempted to analyze this relationship more definitely. If we arrange the species of this genus in the order of their time of

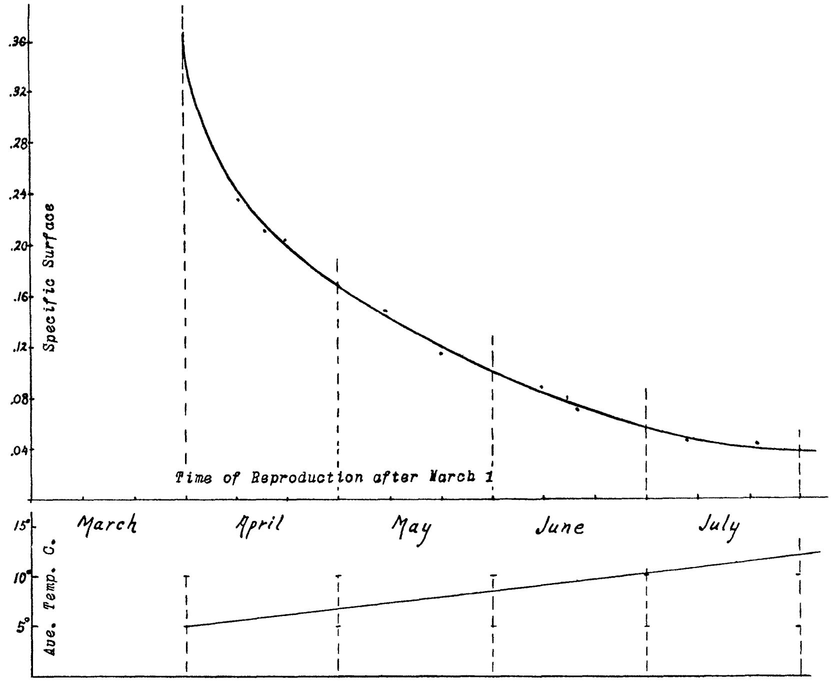

FIG. 2. Above is the curve for the specific surface against the time from March 1 to fruiting. Below is the curve for the temperature against the time to fruiting.

fruiting, we can compare this order with that of the cell diameters, cell volume, and total cell surface. There is no very close coincidence between the order of any of these dimensions and the order of lengths of the vegetative cycle. When, however, the total surface is divided by the volume and these quotients are compared, *i. e.*, when the specific surfaces of the cells are arranged in the order of their magnitude the correlation is very striking, and we are justified in assuming

that the length of the vegetative cycle is an inverse function of the specific surface of the cells. This may be explainable on the basis that the processes of absorption, photosynthesis, proteinsynthesis, and assimilation are limited by the cell surface, while the capacity for accumulation is limited by the volume. Hence other conditions being equal in the cells with the largest specific surfaces we might expect the most rapid approach to maturity (Fig. 2). It has been shown that plant processes are accelerated by temperature, being

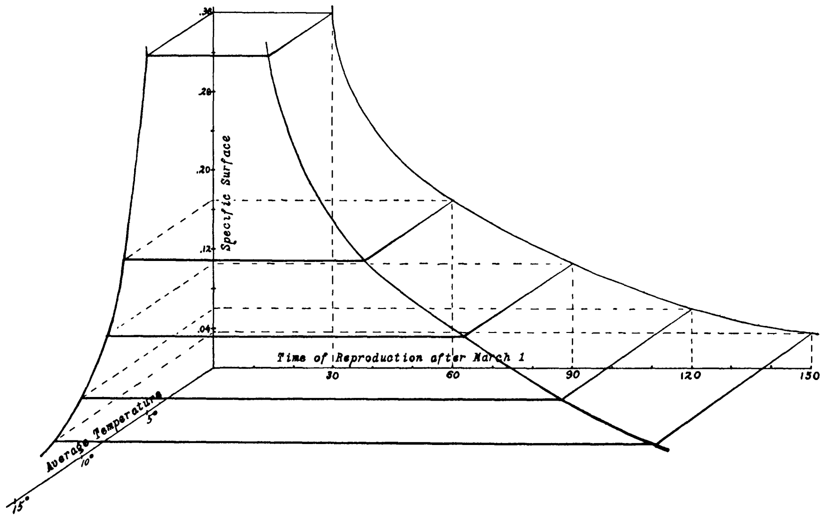

FIG. 3. Curve for the three variables: specific surface, temperature, and time to fruiting.

doubled by a rise of ten degrees. Since the temperature gradually rises during this period a correction must accordingly be made. Nearly all the species germinate in March and for those that fruit in about thirty days the average temperature is about 5° C. For those that fruit in July the average temperature of the whole vegetative cycle is about 12° C. We have then three variables the lengths of the vegetative period, the specific surfaces, and the temperatures. The interrelations of these three variables may be represented by the empirical formula

$$M = \frac{c}{\sigma \frac{t}{10}},$$

in which M is the length of vegetative period, c is a constant, σ is the specific surface, and t is the average temperature. The constant has been found to have a value of 6.5, and the formula may be written $\sigma tM = 65$. Figure 3 presents the interrelations of the three variables. Table I presents some of the average dimensions and other figures upon which the curve was constructed.

TABLE I

In this table the species of Spirogyra are arranged in the approximate order of their fruiting, when germination occurs about March 1. Following are the average dimensions; time of reproduction; approximate temperature of the whole vegetative period; the specific surface; the order by diameters; order by volumes; order by specific surfaces; finally the calculated length of the vegetative period, using the empirical formula $\sigma tM = 65$.

Spirogyra	Average Dimen.	Reprod.	Temp. Veg. Per.	σ	Order Diam.	Order Vol.	Order σ	M ($\sigma tM = 65$)
								days
tenuissima	12 × 120	Apr.	5° C.	.350	1	2	25	37
inflata	18 × 140	Apr.	5°	.236	2	4	24	55
communis	22 × 65	Apr.	5°	.212	3	1	23	61
catenaeformis	26 × 70	May	6°	.182	4	3	22	59
Juergensii	28 × 90	May	6°	.165	5	5	21	67
Weberi	28 × 150	May	6°	.156	5	12	20	69
Grevilleana	30 × 90	May	6°	.155	6	7	19	70
Lagerheimii	30 ¼ 120	May	6°	.150	6	9	18	72
varians	36 × 75	May	6°	.138	8	6	17	78
areolata	34 × 200	May	7°	.127	7	17	16	73
fallax	36 × 150	May	7°	.124	8	13	15	74
protecta	36 × 200	May	7°	.121	8	19	14	76
decimina	40 × 100	May	7°	.120	10	10	13	77
reflexa	38 × 150	May	7°	.118	9	16	12	78
fluviatilis	40 × 140	May	7°	.114	10	15	11	81
porticalis	42 × 130	May	8°	.110	11	14	10	74
condensata	52 × 60	May	8°	.110	13	8	10	74
dubia	46 × 90	June	8°	.104	12	11	9	78
stictica	46 × 240	June	8°	.095	12	20	8	85
novae-angliae	55 × 220	June	9°	.082	14	21	7	88
diluta	78 × 90	June	9°	.073	16	18	6	98
majuscula	60 × 300	June	9°	.073	15	24	5	98
submaxima	86 × 150	June	10°	.059	17	22	4	110
maxima	120 × 120	June	10°	.050	19	23	3	130
setiformis	100 × 200	July	11°	.050	18	25	3	130
crassa	150 × 150	July	11°	.040	21	26	2	147
ellipsospora	140 × 250	July	12°	.036	20	27	1	150

Additional evidence is given for the correctness of this supposition in the fact that in several cases for which I have sufficient data concerning large and small forms of the same species, the dates of fruiting

are here also in harmony with the idea that the length of the vegetative cycle is a function of the specific surface.

Reproduction.—It is evident from the foregoing that in the Zygnemales and probably the Oedogoniales that the length of the vegetative period is the important period for study and experimentation, while the period of sexual reproduction is the supplement to this period. In some of the other orders of algae this period of accumulation seems to be less important and reproduction may be induced at all times by changes in the environment. Zoöspore production is induced in nature by a sudden rise of temperature, and by changes in light. The effect of nutrients and other chemical substances on reproduction cannot be determined from field observations. But when the collections from waters of sand and shale regions are compared with those of the prairie there can be no doubt that the number of fruiting species is very small. The length of the time required for the formation of the gametes, the union of the gametes and the formation of the spore is undoubtedly shortened by a rise in temperature, and lengthened by a lowering of the temperature.

In these more specialized groups, then, the environmental factors operate in general to accelerate, or retard or even inhibit the process of maturing.

One factor, however, deserves especial attention because of the fact that it has been emphasized so many times in connection with the reproduction of algae in nature: the concentration of the water. This matter of concentration has been appealed to both by those who think of it in terms of osmotic pressure, and those who think of it as increasing the mineral nutrients. The same idea is sometimes expressed in terms of the water levels. In all these cases the assumption has been made that the lowering of the water levels in a pond or pool results in the concentration of the pond solution. Three years ago I pointed out that, in general, algae fruit more abundantly during high-water periods than during low-water periods. This statement can be made on a still surer basis to-day than at that time. Now some of Klebs's experiments have shown that the fruiting of algae may be accelerated by increasing the concentration. Perhaps it is these results coupled with the experience of seeing waters in aquaria become concentrated through evaporation that has led to belief in the correlation between concentration and fruiting.

Since my figures ran contrary to this idea that algae fruit when

the ponds are drying up, I made periodic determinations of the freezing points during 1913, 1914 and the spring of 1915. These determinations number somewhat more than two hundred, and it has been possible to see the effects of torrential rains, showers, and the most prolonged droughts known in central Illinois. In general the results indicate that the highest concentrations coincide with the periods of greatest rainfall and higher water levels, and the periods of low concentration are coincident with low water levels and drought. This result may be readily explained since the rains bring in the soluble salts from the upper layers of the soil. But the rains also bring in silt, clay and suspensoids. These require days and weeks to settle but meanwhile they have exposed an enormous surface for adsorption to all parts of the pond solution, and when they finally settle to the bottom they take nearly all the soluble salts with them. Indeed in the autumn of 1913 the Beckmann thermometer scarcely distinguished between distilled water and certain pond solutions. Since the rains in Illinois are mostly in the spring and autumn there are two annual maxima of concentration, one coinciding with the beginning of the spring rains and a lesser one coinciding with the beginning of the autumn rains. In late summer and late winter the concentrations reach their minima. I wish to be clearly understood to apply this statement only to pools, ponds, and streams fed by surface run-off. I have a series of determinations for the underground water of a well and in this case the water reaches its greatest concentration in late summer. This harmonizes with the numerous analyses of our large streams fed by springs and underground water, in which it has been clearly shown that the water concentrates in late summer.

The amount of concentration is also of interest to those who have relied on the osmotic pressure as a factor in producing the reproductive phase. The waters of the ponds and streams which I studied had an osmotic pressure of from one-tenth to one four-hundredth of the osmotic pressure of the cell sap. In the case of the waters, the depression of the freezing point varied from 0.002°–0.043°, in the case of the algae it varied between 0.4° and 0.9°. So that at most the osmotic pressure outside the cell is but a small fraction of the pressure on the inside of the cell.

To return then to my observations on the fruiting of algae as coincident with the periods of high water, these are also the periods of high concentration. And if these results need be in harmony with

the concentration experiments, they are. But it is doubtful whether they need bear any relation to these experiments, for the concentration used is not ordinarily attained or even approached in nature.

The Method of Reproduction.—I have already spoken of the seemingly slight changes in conditions which initiate the production of zoöspores. In nature they are for the most part produced during the earlier part of the vegetative period. I wish to speak more particularly regarding the reproduction in the Zygnemales. As is well known conjugation may occur between cells of the same filament (lateral conjugation), or between cells of different filaments (scalariform conjugation), or they may produce aplanospores without conjugation. This last method I have found to be much more common than has been hitherto supposed. The question arises, are these different methods of reproduction controlled by environmental factors or do they indicate different hereditary strains of the species? Field observations point to the conclusion that they are hereditary qualities rather than effects of the medium in which they grow. The evidence may be summarized as follows:

1. All three modes of reproduction, indicated above, may be found in adjacent cells of the same filaments; (2) the three forms of reproduction may occur simultaneously in different species making up a single small mass of algae; (3) in certain ponds certain species have been found annually, producing only aplanospores, in other similar ponds producing only zygospores or both; (4) in several species of Zygnemales the conjugation may be almost entirely lateral in one mass collected and just as completely scalariform in another. Without a knowledge of the field conditions these last two proofs may seem as good evidence for the other side, but knowing the conditions under which these differences occur I think no one would question the interpretation given here.

Summary.—In conclusion, I wish to summarize the more important facts brought together in this study of algal periodicity.

1. Although algae germinate, develop vegetatively, and produce spores throughout the year, they may be conveniently grouped, on the basis of their *complete* life histories, into winter annuals, spring annuals, summer annuals, autumn annuals, ephemerals, and perennials.

2. The contradictory results of experimenters on the production of spores in the algae may be due to the neglect of the normal periodicity and vegetative age of the algae used in the experiments.

3. Four distinct periods may be recognized in the life history of most fresh-water algae: germination, vegetative development, reproduction, and dormancy.

4. The great majority of zygospores, oöspores, and aplanospores germinate in the spring. There is germination going on however at all times, and a secondary maximum occurs in the autumn.

5. The factors involved in the germination of the spores are probably as numerous as those initiating germination in seeds. The importance of temperature has probably been overestimated.

6. The length of the vegetative period in some forms is quite indefinite. In the Zygnemales and Oedogoniales it probably has a definite length under normal conditions.

7. Temperature, light intensity, concentration and mineral content of the water accelerate or retard the approach of the reproductive period.

8. The normal length of the vegetative cycle in Spirogyra is an inverse function of the specific surface of the cells. This is possibly also true in Zygnema and Oedogonium.

9. The normal length of the vegetative cycle in species of Spirogyra is approximately equal to a constant (65) divided by the specific surface times the temperature.

10. The concentrations of the waters in pools, ponds and surface streams attain their maxima in early spring and autumn, corresponding in general with the periods of heavier rainfall.

11. The lowest concentrations occur in late winter, and at the end of a prolonged drought in summer.

12. The periods of most abundant fruiting of algae correspond with the periods of high water levels.

13. The concentration of natural waters at their maximum is so small in comparison with the concentrations of the cell sap that it is doubtful whether it is of any significance in initiating reproduction.

14. In the Zygnemales, lateral conjugation, scalariform conjugation and aplanospore production appear to be hereditary tendencies rather than the result of environmental conditions.

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